Encarsia transvena (Hymenoptera: Aphelinidae) Development on Different *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) Instars

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ABSTRACT *Encarsia transvena* is a potentially useful parasitoid of *Bemisia tabaci* (Gennadius) in India. Development, host preference and parasitism by the parasitoid were studied at 25–30°C and 70–75% RH. Results showed that *E. transvena* is a solitary, arrhenotokous, heteronomous, autoparasitoid. Female eggs are laid internally in whitefly nymphs and develop as primary parasitoids. Males develop as hyperparasitoids, either on females of their own species or on other primary aphelinid parasitoids. Both sexes have an egg, three larval, a prepupal and pupal stage. Development from egg to adult took 11.3–15.0 d for females and 12.1–14.6 d for males. Superparasitism was common under cage condition, either on specific females or other primary parasitoids. *E. transvena* females were able to develop in all *B. tabaci* nymphal stages but preferred the third and early fourth instars. Oviposition and developmental periods of the parasitoid were longest on first and fourth (late) instars of *B. tabaci*. The highest percentages of parasitization occurred in third instar and fourth (early) instar *B. tabaci* and the lowest percentages in first and fourth (late) instars. The information should be useful in designing mass rearing protocols and in release trials for suppression of *B. tabaci* populations.

KEY WORDS *Encarsia transvena*, *Bemisia tabaci*, parasitoid, hyperparasitoid, superparasitism, host suitability

THE SWEET POTATO WHITEFLY, *Bemisia tabaci* (Gennadius) is a major pest and plant virus vector attacking a wide variety of food, and vegetable crops throughout India. Outbreaks were reported in southern India during 1985–1987 and northern India during 1987–1995, on cotton, egg plant, tobacco, bhendi, tomato and several ornamental plant species (Palaniswami et al. 2001). *B. tabaci* has been reported as a pest on >600 crops and weed hosts and as a vector of 70 plant-infecting viruses in tropical and sub-tropical countries (Hunter and Poston 2001). Management of *B. tabaci* is challenging because of its intercrop movement, high reproductive potential, broad host range, resistance to insecticides and its underleaf habitat. Rao et al. (1989) showed that nymphal parasitism of *B. tabaci* due to aphelinids reached 40% in two years on untreated cotton in Andhra Pradesh, whereas in insecticide treated cotton, parasitism was reduced to 9.7% (Rao et al. 1990).

Parasitic wasps of three genera, *Amitus*, *Encarsia* and *Eretmocerus*, are among the most important natural enemies of the *B. tabaci* complex (Cock 1986, Hoelmer 1995). Studies carried out by Heinz and Parrella (1998) showed that the percentage of parasitoids successfully developing to adults was greater for *Encarsia* than for *Eretmocerus*, independent of host.

There are over 170 species in the genus *Encarsia* worldwide (Hayat 1989). *Encarsia transvena* was first described by Timberlake (1926). It is the most commonly occurring *B. tabaci* parasitoid in India on cotton, eggplant, tobacco, cassava and sweetpotato. In India, *E. transvena* (as *E. flava*) was first reported by Shafeei (1973). *Encarsia flava* is considered synonymous with *E. transvena* (Polaszek et al. 1992). Natarajan (1990) reported *E. transvena* (as *E. shafeei*, also synonymous) as an important parasitoid of *B. tabaci* on cotton during 1985–88 in Tamil Nadu. Lal (1980) and Palaniswami and Pillai (1990) reported that *E. transvena* (as *E. flava*) and *B. tabaci* populations occurred throughout the year in cassava ecosystems. Kapadia and Puri (1990) reported that *E. transvena* was the most important of six aphelinid parasitoids recorded on *B. tabaci* in India. Under Maharashtra conditions (RH 50–60%, maximum temperature 30–40°C), *E. transvena* parasitized 25–63% of *B. tabaci* nymphs. Gerling (1983) and Kapadia and Puri (1990) reported on the biology of *E. transvena* in the laboratory and the field. The present studies were conducted to fill in information gaps on female and male parasitoid development, the suitability of *B. tabaci* instars for parasitoid development, and the extent of parasitism occurring in different *B. tabaci* stages of development.

Materials and Methods

Encarsia transvena was identified by Mohammad Hayat (Aligarh Muslim University, India), and voucher specimens have been deposited in the Division of Crop

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Host/Parasitoid Culture. *Bemisia tabaci* pupae were collected from sweet potato and cassava plants in the field. The separate collections were held in a screen house. Emerged adults were released on their respective host plants in cages. The angle iron frame cages were 70 cm (height) x 42 cm Square and covered with organdy cloth on three sides. A transparent plastic sheet covered the remaining side and the cage top. The established whitefly colonies were maintained separately on cassava and sweet potato in the screen house (Temperature 25–30°C, RH 70–75%) in cages for parasitoid rearing.

E. transvena cultures were established by collecting parasitized pupae from the field. They were brought to the screen house and placed in petri dishes with 10% honey as parasitoid food following emergence. Emerged adult parasitoids were released on caged sweet potato and cassava plants infested with *B. tabaci* nymphs. Parasitized black pupae were sexed as females when meconium was near the vasiform orifice only, and as males when there was additional meconium on both sides of the posterior periphery. Virgin female parasitoids were obtained by confining female black pupae in vials. Upon emergence, female parasitoids were placed on a detached sweet potato leaf with abundant whitefly nymphs for ≈6 h. The detached sweet potato leaf was confined in a petri dish, and the leaf petiole was covered with moist cotton to retain leaf turgidity. Parasitoids obtained sufficient nutrients for egg laying by feeding on honeydew and the body fluid of whitefly nymphs, which oozed out of ovipositor punctures. Mated female parasitoids were obtained by confining a newly emerged female with two males in a petri-dish for ≈6 h. Two-day-old females were used in all experiments.

Eretmocerus mundus (Mercet) was reared separately on *B. tabaci* on sweet potato. Prepupae and 'red eyed pupae' of *Er. mundus* collected from the stock culture were used for *E. transvena* male development studies.

Life-History and Development Time. Approximately 50 adult whiteflies were released into each clip cage (4-cm diameter) placed on sweet potato leaves. After 24 h, all whitefly adults were aspirated out and the leaf portion enclosed by the clip cage marked with indelible ink. The plants were placed in insect proof cages until the nymphs developed to third and early-fourth instars. Three *E. transvena* mated females were introduced into a 4-cm diameter clip cage placed on sweet potato leaves infested with whitefly nymphs. After 48 h, the clip cage with parasitoids were removed and leaf portion enclosed by the clip cage marked with indelible ink, and plants were kept undisturbed in rearing cages. On each subsequent day, several randomly selected *B. tabaci* nymphs were dissected until egg, first, second and third instars of *E. transvena* were obtained (≈7–8 d). Parasitoid development time was counted from the day the female parasitoid was released. Egg period (egg to first instar emergence) was determined when the first instar was observed during

dissection. Development times for second instar, third instar, prepupa, and black pupa were determined in the same way. All stages were photographed using a Leica M10 stereo microscope equipped with an image analyzer system. A total of 1980 nymphs were exposed to parasitoids for ≈48 h. 55 nymphs were observed for each parasitoid stage, and each experiment was repeated six times.

Male development was studied by releasing two unmated *E. transvena* females on five different stages; third instars (in dry environment), prepupae and early black pupae of *E. transvena*, as well as prepupa and 'red-eyed pupa' of *Er. mundus*. When a female third instar fed upon the contents of a whitefly, a dry host environment was formed. This dry host environment extended through the prepupal and pupal stages of the parasitoid. We chose these stages because earlier work suggested that the *E. transvena* female prefers to oviposit unfertilized eggs in *B. tabaci* nymphs in dry environments (Gerling 1983, Hunter and Kelly 1998). 20–30 individual whiteflies of each of five different stages were exposed to newly emerged unfertilized female *E. transvena*. After 48 h, female parasitoids were removed and plants were kept undisturbed in cages. After 24 h, the five different host stages were collected and kept separately on microscopic slides in petri dishes. Development time for different stages was recorded as described above, by observation through the stereo microscope at up to 800× magnification. Larval development was photographed. Morphometrics of different stages of female and male parasitoids were taken using a Leica compound microscope, and the means of six replications are presented.

Host Stage Suitability and Parasitism. We examined which stage of *B. tabaci* was suitable for parasitoid oviposition. Approximately 30–50 adult whiteflies were released into each clip cage placed on sweet potato leaves. After 24 h all the whiteflies were aspirated from the clip cages and the area of the leaf covered by the clip cages marked with indelible ink. The egg-infested plants were confined in insect-proof cages, and host stages were allowed to develop to the desired instars (first (sedentary), second, third or fourth instars). Fourth instars were divided into early fourth instar nymphs (flattened, translucent and 'red eyes' not well developed) and late fourth instar nymphs (opaque, bulged and with well developed 'red eyes'). When the desired host stage was reached, 30–50 different-stage nymphs were exposed to three mated *E. transvena* parasitoids held in a 4-cm diameter clip cage. Clip cages with parasitoids were removed after 48 h and plants left in cages. Whenever a black pupa was formed, it was removed and placed in a petri dish. Development time from egg to black pupa and black pupa to adult *E. transvena* emergence were recorded separately on all host stages. Parasitism percent was recorded from all *B. tabaci* stages. Total development time from egg to adult emergence also was recorded from the same observations. Percent of successful adult parasitoid emergence was calculated based on the number of adult parasitoids emerged and

the total number of black pupae recorded, separately for each stage of *B. tabaci.*

Statistical Analysis. Results of development time, host stage suitability and percentage of parasitism on different instar nymphs were analyzed using one-way analysis of variance (ANOVA) and means were compared using the Waller Duncan Posthoc multiple comparison test (SPSS, 1989). Significant mean differences were accepted at the 0.05% probability level.

All experiments were repeated six times and were carried out in a screen house condition at 25–30°C and 70–75% RH. Sweet potato and cassava varieties used in all experiments were *Sree Nandini* and *M4 & H226,* respectively.

Results

Development Time. The development of *E. transvena* from egg deposition to adult at room temperatures of 25–30°C and 70–75% RH was ≈11.3–15.1 d for females and 12.1–14.6 d for males. The developmental stages were eggs, three larval instars, prepupa and black pupa (Fig. 1 and 2).

Females. A female parasitoid stands over the host body and penetrates the dorsal cuticle with its ovipositor and lays an egg. Eggs averaged 0.161 ± 0.012 mm long and 0.046 ± 0.006 mm wide. Polar bodies were visible in the newly laid eggs (Fig. 1a). Egg development to the first instar occurred in 2–3 d. During this time egg contents changed, and migrating cleavage nuclei were observed in the peripheral region (Fig. 1b). First instars were transparent, 0.207 ± 0.009 mm long and 0.081 ± 0.007 mm wide. They had 13 body segments, three thoracic and 10 abdominal. During early first instar development the segments were not visible. The head had a notch containing a sickle-shaped mandible. The larvae were observed moving within the body fluid of the host. The first instar has a 0.034 ± 0.012 mm long tail with no protuberance (Fig. 1c). The time of development from first to second instar was 2 d. The second instar averaged 0.345 ± 0.030 mm long and 0.092 ± 0.007 mm wide, and segment 13 had a small button-like structure. The cuticle is transparent and most of the internal organs were visible through it.

Development from the second to third instar occurred in two days. In the late second instar, remnants of the cast skin were observed loosely attached to the last abdominal segments (Fig. 1d). The third instar measured 0.552 ± 0.020 mm long and 0.130 ± 0.009 mm wide and was clearly distinguishable (Fig. 1e). Development of third instar took place in a semidry environment to dry environment of whitefly host. Nine pairs of spiracles, two on the thorax and seven on the abdomen were observed at a magnification of 800x (Fig. 1f). Third instar larvae completed development in two days. During this interval larva depleted the contents of the host body (making a dry environment), yellow-colored meconium changed to light brown and was visible through the nymphal cuticle. Larvae were sickle-shaped and the ileo-labial gland was visible through the ventral side of the larvae (Fig.

1g). Third instar larvae moved to the anterior wall of the host puparium. Two to five dark brown meconial pellets were deposited along the host puparium wall on either side of the host vasiform orifice (Fig. 1h) in the prepupal stage. Prepupae were ash-colored with no organs visible through the cuticle. Prepupae completed development to black pupae in 24 h (Fig. 1i).

Black pupae averaged 0.575 ± 0.030 mm long and 0.391 ± 0.027 mm wide. Female pupae completed development in 5–7 d. Outlines of head, eyes, wing pads and legs were visible (Fig. 1j). Late in pupal development, a distinct head, red ocelli, dark red colored eyes, antennae, wings and legs were visible through the host puparium. Before emergence, the black pupal cuticle was shed revealing the orange body, red ocelli, reddish black eyes and fully developed wings and legs. Pupa faces the venter of the host, turns over to face antero-dorsum of host. Adult emergence occurred through a hole chewed by the adult in the antero-dorsum (Fig. 1k). Adult parasitoid made its emergence hole in 20–30 min for its exit from the whitefly puparium.

Males. Male eggs (unfertilized) were laid externally over an immature female parasitoid enclosed within *B. tabaci* puparia (Fig. 2a). We observed successful male development in third instars (in dry environment), prepupae and early-stage female *E. transvena* black pupae, and prepupa and 'red-eyed pupa' of *Er. mundus.* The externally-laid male egg was generally attached to prepupal and early pupal stages of both parasitoids or found free in the *B. tabaci* puparium. In third instar *E. transvena,* male eggs were sometimes found attached to the body of the female parasitoid host or free in *B. tabaci* puparium (Fig. 2b). Eggs were sticky and averaged 0.117 ± 0.035 mm long and 0.051 ± 0.018 mm wide. Development to first instars occurred in 3–4 d. Usually a single egg was attached to the host; but superparasitism (Fig. 2c) was observed especially in third instar and prepupal stages of female *E. transvena.*

First instar male parasitoids had 13 segments and averaged 0.148 ± 0.017 mm long and 0.060 ± 0.004 mm wide. No segmentation was observed during early development. First instars completed development in 2–3 d. At this stage, the host female parasitoid larva becomes paralyzed and growth ceases. Hyperparasitized larvae were observed feeding externally on the primary parasitoid. On *E. transvena* and *Er. mundus* prepupal stages, hyperparasitized first instars fed on the middle, right side of the host, gradually moving to the anterior (Fig. 2d and e). However, the position of first instar feeding depended on where the parasitoid eggs were laid.

Male second instar parasitoids (Fig. 2f) averaged 0.261 ± 0.010 mm long and 0.077 ± 0.010 mm wide. During the two days of development to third instars, they consumed most of the anterior portion of the host (Fig. 2g). Third instars averaged 0.445 ± 0.110 mm long and 0.150 ± 0.040 mm wide. Development also occurred in two days, and the remains of the host were consumed (Fig. 2h). Meconium appeared in the prepupa as brown-colored pellets on either side of the
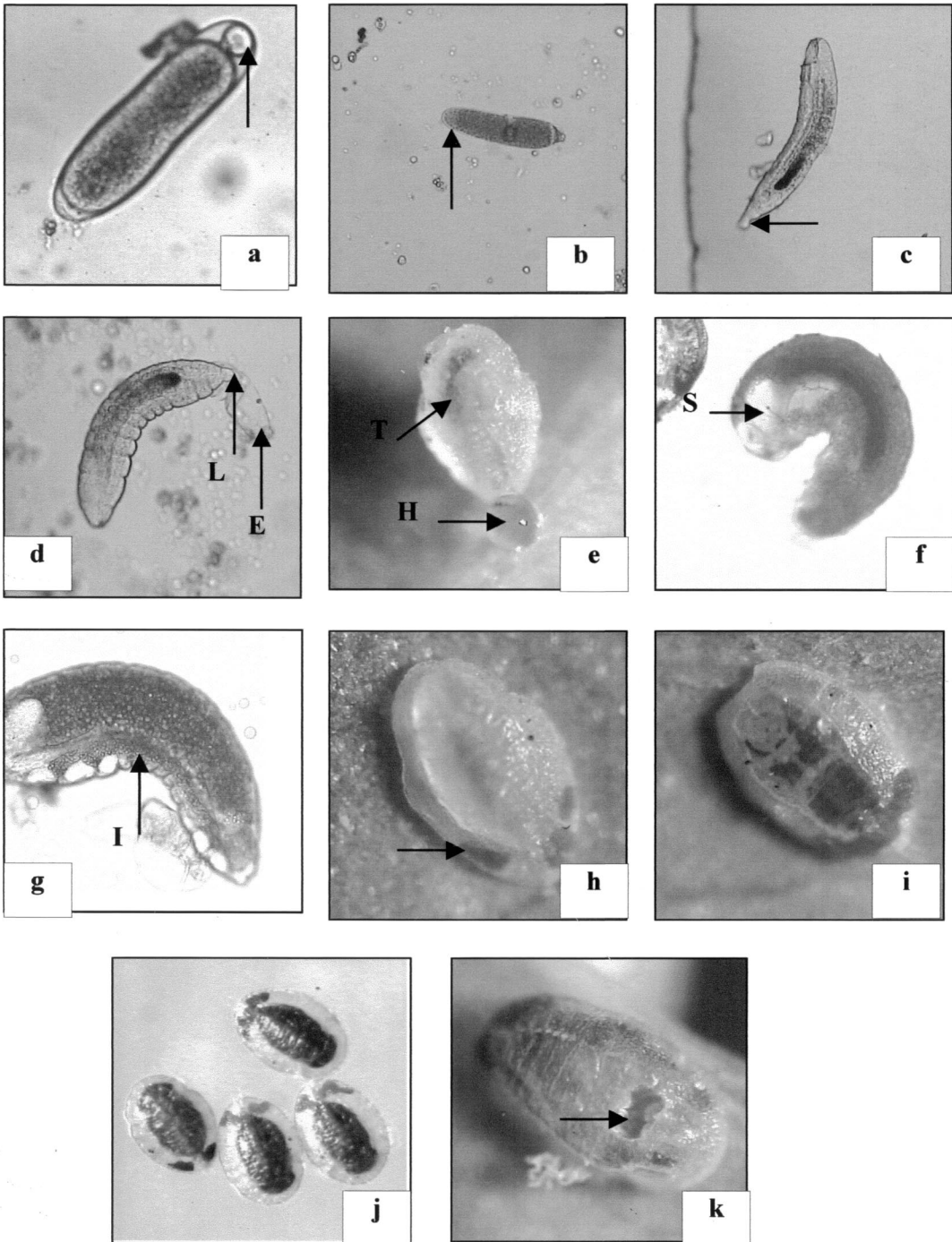
Fig. 1. (a–k) Development of female *Encarsia transvena*; (a) Newly laid female egg, arrow-polar body; (b) Egg development, arrow-migrating cleavage nuclei; (c) First instar, arrow-tail; (d) Second instar, L-last segment, button like appearance; E-exuviae of first instar larva; (e) Parasitized *Bemisia tabaci* first instar larva continue to develop and secrete honey dew, T-third instar, H-honey dew; (f and g) Third instar larva, S-spiracle, I-Ileolabial gland: (h) Prepupa, arrow-meconium: (i) Cocoon formation: (j) Black pupa: (k) Adult making exit hole (arrow).

B. tabaci vasiform orifice (Fig. 2i). In hyperparasitized *E. transvena* (prepupa and early black pupa) two groups of the meconial pellets were formed. But in hyperparasitized *E. transvena* third instars, only one group of meconial pellets occurred. Remnants of the devoured female *E. transvena* larvae were visible and
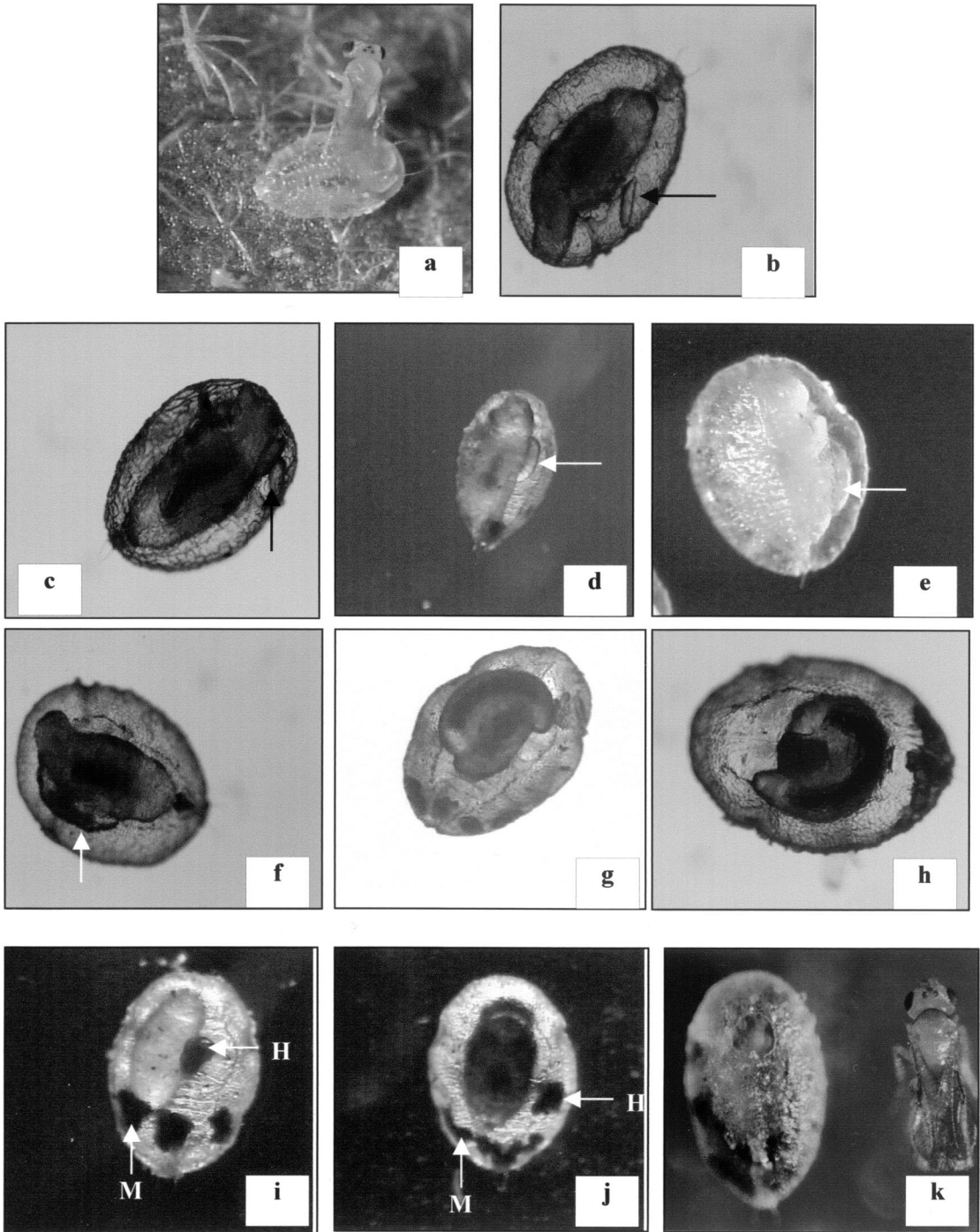
Fig. 2. (a–k) Development of male *Encarsia transvena*; (a) *E. transvena* laying male egg; (b) Male egg on third instar (dry environment), arrow male egg; (c) Superparasitism (arrow); (d) First instar (arrow), e) First instar (arrow) on *E. mundus* prepupa; (f) Second instar (arrow), (g) Third instar; (h) Third instar consumes the host; (i) Prepupa, H-remains of the host; M-meconium; (j) Black pupa, H-remains of the host; M-meconium; (k) Newly emerged male *E. transvena*.

distinct in the parasitized whitefly nymphs (Fig. 2i and j).

The pupal period of male *E. transvena* was com-

pleted in 4–5 d. During pupal development, appearance of a distinct head, body segments and development of adult coloration, formation of reddish black

Table 1. Developmental time (days) of *Encarsia transvena* on different stages of *Bemisia tabaci*

Parasitoid stage	*B. tabaci* instars (Mean ± SE)				
	1st (n = 650)	2nd (n = 323)	3rd (n = 402)	Early 4th (n = 226)	Late 4th (n = 636)
Egg to black pupae	10.58 ± 1.43a	9.58 ± 1.56ab	7.20 ± 0.41c	7.50 ± 0.71c	9.25 ± 0.69b
Black pupae to adult	6.92 ± 0.86ab	6.00 ± 0.55bc	5.42 ± 0.49c	5.66 ± 0.68bc	6.58 ± 0.59a
Total	15.08 ± 0.86a	14.33 ± 1.40ab	11.25 ± 1.04c	11.40 ± 0.94c	13.92 ± 0.86b

n = Total number of individuals observed.

Numbers in each row followed by the same letter are not significantly different (at $P < 0.05$ level) based on ANOVA and Waller-Duncan Post-hoc multiple comparison test.

eyes, wings and red colored ocelli were observed (Fig. 2j). Before emergence, the pupal cuticle was shed. Pupa facing the host venter turned over to face the dorsal side of the whitefly puparium and adult parasitoid chewed a hole in the host dorsal wall to escape (Fig. 2k).

Host Instar Suitability and Parasitism Percentages. *E. transvena* parasitized all nymphal instars of *B. tabaci*, and pupation and adult emergence took place in all host stages (Table 1). The development of female *E. transvena* from egg to black pupa was significantly faster when oviposition took place on third and early fourth instars compared with the development in first, second and late fourth instars. Time taken for egg to develop black pupa was significantly longer in *B. tabaci* first instar followed by second and fourth (late) instars and shorter in third and fourth (early) instars ($F = 12.53$; df = 4, 30; $P < 0.001$). The longest pupal period (black pupa to adult emergence) occurred in first instars (6.9 d). We observed that parasitized first instars of *B. tabaci* continue to grow and secrete honeydew (Fig. 1e), whereas parasitized third and early-fourth instars ceased development with no honeydew secretion. Pupal development time in second, third and fourth instars was not significantly different ($F = 6.52$; df = 4, 30; $P = 0.001$). Total development averaged 15.1 d on first instar *B. tabaci*, 13.9 d on late fourth instar, and 11.3 and 11.4 d on third and early fourth instars, respectively. Total development was shortest in third instar and was on par with fourth (early) instar. It was longest in second and fourth late instars ($F = 18.77$; df = 4, 30; $P < 0.001$) (Table 1).

Parasitism percentages were significantly higher on third and early fourth *B. tabaci* instars than on first, second and late fourth instars. The highest rate of parasitism was on third instars (51.7%) followed by early fourth (42.0%). It was significantly lower in first and late fourth instars (13.9% and 16.5%, respectively) and were on par with each other (Fig. 3). Parasitism percentage on second instar was 25.9% and was on par with that of fourth late instar ($F = 19.68$; df = 4,30; $P < 0.001$). When *E. transvena* parasitized third and fourth (early) *B. tabaci* instars, successful adult parasitoid emergence was 98.2% and 94.7%, compared with 48.2, 50.1 and 41.7% for first, second and late fourth instars, respectively.

Discussion

Encarsia transvena is a potential and dominant parasitoid of *B. tabaci* in India (Palaniswami et al. 2001). Our studies revealed that *E. transvena* is a heteronomous autoparasitoid. Females developed as primary parasitoids on all stages of *B. tabaci* and males as hyperparasitoids on conspecific females (*E. transvena*) and heterospecific females (*Er. mundus*). In the present investigation, development of *E. transvena* from egg deposition to adult was 11.3–15.1 d for the females and 12.1–14.6 d for the males. The results agree favorably with those of Gerling (1983), 15 d, and Kapadia and Puri (1990), where development ranged from 8.1 to 18.7 d.

Even though male and female larvae were almost similar in external appearance, some differences were observed in the male larvae, which might be due to its nature as secondary parasitoid and also due to the competition with either conspecific, or heterospecific larvae. As reported for *E. porteri* (Hunter et al. 1996), first and second instars of male *E. transvena* were enclosed within a transparent membrane, which was absent in female larvae. Unlike male larvae, female larvae were found to move within the body fluid of the host. Male larvae were found to attach and feed on the body of the primary parasitoid, and were usually sticky in nature. Female first instar of *E. transvena* has a long tail, but unlike first instar of *E. pergandiella* (Gerling
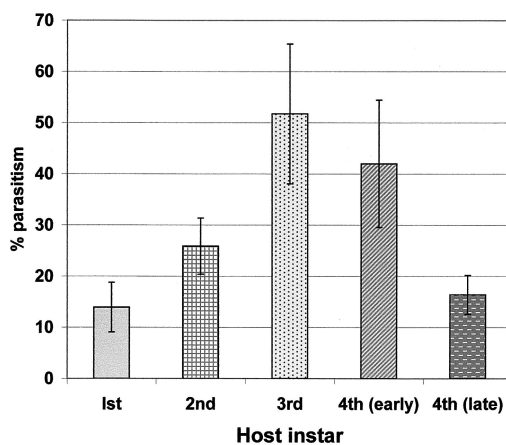

Fig. 3. Percent parasitism of *Bemisia tabaci* instars by *Encarsia transvena* (Mean ± SD).

1983), the tail has no protuberance. Head of *E. transvena* has a notch containing sickle shaped red colored mandible similar to that reported in *E. pergandiella* (Gerling 1966).

Usually single male egg was found to attach to the primary host. But occasionally we observed superparasitism in all the host stages that we offered for male developmental studies. Gerling and Foltyn (1987) reported that superparasitism occurred when host discrimination efficiency was reduced. Wylie (1983) found that parasitoid larvae took longer to develop in superparasitized hosts than in singly parasitized hosts. Van Alphen and Visser (1990) suggested that having two (or more) eggs in a host might increase probability of producing an offspring compared with single eggs. In our studies, superparasitism was rare in field collected *E. transvena* and the highest superparasitism occurred in the mass rearing cages with abundant host material. This agrees with the report of Hunter and Goldfray (1995) that the male eggs were produced only when hosts were abundant. Hence, the male/female ratio seems to depend on female abundance.

E. tricolor (Avilla and Copeland 1987) and *E. pergandiella* (Gerling 1966) parasitized all four instars of *B. tabaci* and *Trialeurodes vaporariorum* (Westwood), respectively. Nell et al. (1976) also reported that *E. formosa* Gahan parasitized all instars of *T. vaporariorum.* Our results showed that *E. transvena* successfully parasitized all *B. tabaci* nymphal instars, but the rates of parasitism and development were different in different instars.

Parasitism percentages were significantly higher on third and early fourth instars than on first, second and late fourth instars. Van Alphen et al. (1976) observed that even though *E. formosa* laid eggs on all *B. tabaci* instars, third instars and prepupae were preferred for oviposition. Lopez Avilla (1988) reported that *E. formosa, E. luteola, E. adrinae,* and *E. cibcenses* parasitized all instars of *B. tabaci;* but the third instars had the highest percentage of parasitization. Similar results were observed for *E. pergandiella* (Schuster and Price 1996, Jones and Greenberg 1999).

Our results suggest that development time of *E. transvena* was shortest in third and early fourth instars (with maximum parasitoid adult emergence), and longest in first and late fourth instars. The lengthening of the egg and larval development period in young host also has been reported in other heteronomous aphelinids (Walter 1983). We observed that parasitized first instars of *B. tabaci* continue to grow and secrete honeydew. A similar observation was reported in *E. formosa* (Arakava 1982) and in *E. pergandiella* (Jones and Greenberg 1999). When *E. transvena* parasitized first, second or third instar *B. tabaci* in the current study, the parasitoid could be classified as koinobiont (Askew and Shaw 1986), because the host continued to feed, grow, develop and secrete honeydew after parasitization. However, when *E. transvena* parasitized third and fourth instars, we observed that, the host evidently stopped development, as is characteristic of idiobiont parasitoid. Hoddle et al. (1998) reported that *E. formosa* development extended beyond the first instar until the host developed to the fourth instar. Similar observations were reported in *E. pergandiella* (Jones and Greenberg 1999). In our studies *E. transvena* preferred to lay eggs in third and early fourth instars of *B. tabaci,* when all the host stages were available. But when eggs were laid on first or second instars, development slowed until the host reached the third or fourth instar.

The longer period of first instar development may result in higher parasitoid mortality. To avoid this situation, female parasitoids may prefer to lay eggs in third and early fourth instars of *B. tabaci.* Additional studies need to be conducted to determine whether female parasitoids are able to identify the developmental stages of *B. tabaci* by cues emitted from the hosts. Information derived from this investigation contributes to a greater understanding of the *B. tabaci*-parasitoid relationship, and may be useful during mass rearing of *E. transvena.*

Acknowledgments

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